

KLAINEDOXA (IRVINGIACEAE) AT MAKOKOU, GABON: THREE SYMPATRIC SPECIES IN A PUTATIVELY MONOTYPIC GENUS¹

ALWYN H. GENTRY²

ABSTRACT

This paper, in effect constituting a revision of the genus *Klainedoxa*, is a byproduct of ecological studies of tropical forest diversity carried out at the CENAREST laboratory near Makokou, Gabon in 1981. Collections from the rain forest canopy included at least 69 taxa new to the field station, a number new to Gabon, and several apparently undescribed species. In the case of *Klainedoxa*, as well-known but taxonomically difficult genus of large trees, these collections indicate a clear resolution of the heretofore problematical taxonomic relationships.

Canopy trees and lianas of the tropical rain forest are notoriously poorly understood taxonomically, in large part because the difficulty of collecting them has led to a dearth of herbarium material. New techniques for collecting canopy plants, which have recently been developed in Amazonia but little used elsewhere, were critical to the study reported here. Collections of canopy trees and lianas at Makokou were made by using a tree-climbing bicycle (Forestry Suppliers cat. no. 27170) to reach the canopy and a lightweight set of aluminum tree trimming poles (available from the Missouri Botanical Garden) to reach flowering or fruiting outer branches. A similar technique using a movable platform to climb into the canopy has previously been used successfully to collect specimens of large trees at Makokou (Hladik & Hallé, 1973, pl. 3). However, the system employing a tree bicycle (which can climb trees up to 65 cm in diameter) and telescoping tree-trimming pole (potentially 12 m long) is both much more flexible and less physically demanding. Another relevant problem arises when taxonomic work, as has often been the case for tropical plants, is restricted to the herbarium with little communication between systematists and the foresters, ecologists, or native peoples who may know plants in the field and be well aware of obvious differences in characters such as those of large fruits that are rarely preserved in the herbarium. As a rule, and within a single geographic area, one who knows plant

populations intimately in the field, no matter what his training, is likely to be able to evaluate what constitutes a species better than the most eminent herbarium taxonomist. The work reported here draws heavily on the field experience of the team of vertebrate ecologists working at the Makokou laboratory.

Klainedoxa, a small genus of tropical African canopy and emergent trees with large elephant-dispersed fruits, epitomizes these problems. Recent treatments (Aubréville, 1962; Gilbert, 1958) of the genus, variously treated as belonging to Irvingiaceae or to Simaroubaceae, have recognized two species, *K. gabonensis* Pierre ex Engl. and *K. busgenii* Engl., the latter differentiated by its generally larger, more cordate leaves. The "Flora of West Tropical Africa" (Hutchinson & Dalziel, 1958) recognized, in addition to the widespread *K. gabonensis*, an unnamed *Klainedoxa* designated as "imperfectly known." Since *K. busgenii* proves to be no more than an extreme form of variable *K. gabonensis* (Letouzey, pers. comm.), *Klainedoxa*, as currently understood, would seem to contain only a single highly variable species.

The forest surrounding the field station at Makokou, Gabon is one of the best known areas of tropical Africa floristically (Hallé, 1964, 1965; Hallé & Le Thomas, 1967, 1970; Hladik & Hallé, 1973; Florence & Hladik, 1980). Nevertheless, only a single species of *Klainedoxa* has been reported to occur at the field station (Hallé & Le

¹ I thank Drs. A. Hladik, R. Letouzey, P. Raven, and L. Emmons for reviewing the manuscript; Dr. Emmons for originally pointing out to me the three different *Klainedoxa* fruit types; and Paul Posso and the Institut de Recherche sur L'Écologie Tropicale (CENAREST) for making possible my field work in Gabon. This research was supported by grants from the Explorers Club and National Geographic Society.

² Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

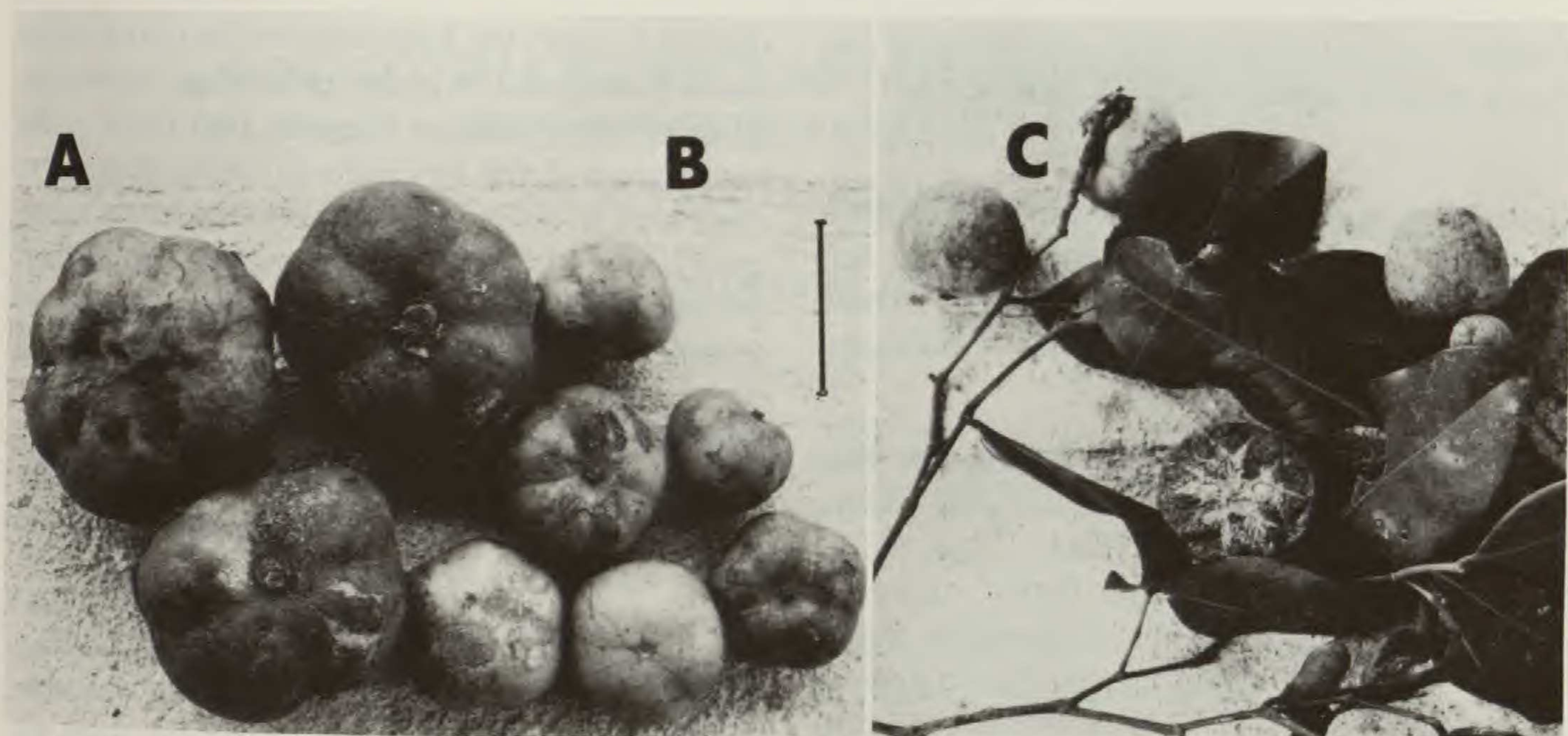


FIGURE 1. Fruits of *Klainedoxa* at Makokou, Gabon.—A. *K. gabonensis* (large fruits).—B. *K. trillesii* (small fruits).—C. *K. microphylla*. Line is 4 cm.

Thomas, 1967), although Florence and Hladik (1980: 237) mention two sympatric "forms" of *Klainedoxa* of unspecified taxonomic rank, and ecologists working there discriminate three different types of *Klainedoxa* fruit on their study grid (Emmons, pers. comm.; Fig. 1). The common species at Makokou is *K. gabonensis* [Gentry 33303A, 33779 (MO)], which has large, 5-lobed, depressed-globose fruits 4–4.5 cm long and 5–7 cm wide that remain green at maturity, and ovate acute-tipped leaves that are 7–20(–30 in juveniles) cm long. This emergent tree is one of the best known and most distinctive plants of tropical Africa.

A second species [Gentry 33183, 33508 (MO)], also an emergent giant, has distinctly smaller fruits that are only 2–3 cm long and 3–4 cm wide though of a similar depressed-globose, 5-angled shape. The smaller seeds, though still hard-shelled, are possible to cut with a plant clipper, unlike those of *K. gabonensis*. This species has leaves similar in shape to those of *K. gabonensis* but smaller [(5–)7–9(–11) cm long]; although there is some overlap between the two species, most leaves of all collections of *K. gabonensis* are more than 9 cm long. The fruits of this small-leaved small-fruited plant often turn yellow at maturity unlike those of *K. gabonensis* (Emmons, pers. comm.).

The third type of fruit [Gentry 33178, 33182 (MO)] is even more distinctive. It is globose, unlobed, glaucous gray-green in color, and 3.5–4.5 cm in diameter. The leaves of this species

are also distinctive in being obtuse apically, elliptic to obovate in shape, and small (8–10.5 cm by 4.5–6 cm). All three of these plants occur along trails in the main ecological study grid at Makokou and no intermediates between them have been observed. All key out to *K. gabonensis* in the "Flore du Gabon" (Aubréville, 1962).

A survey of the literature reveals that 20 names have been proposed for different collections of what is now generally treated as *K. gabonensis* sensu lato. Van Tieghem (1905) proposed 14 specific epithets for *Klainedoxa*, basing them largely on vegetative characters, and several additional species were proposed subsequently by Engler (1907, 1911) and others. Pellegrin (1924) reviewed the species and accepted nine of them, still based almost entirely on vegetative characters. Letouzey (1975 and pers. comm.) has recognized two taxa in Cameroun, the second treated as *K. gabonensis* var. *microphylla* but now considered by him to constitute a distinct species.

Two of the extant synonyms clearly are applicable to the two nameless Makokou species. *Klainedoxa trillesii* was characterized by exactly the same combination of smaller leaves and much smaller fruits than *K. gabonensis* that marks the small-fruited Makokou taxon. *Klainedoxa gabonensis* var. *microphylla* is characterized by the small, blunt-tipped leaves that mark the glaucous-fruited Makokou plant. Since there is no doubt that this represents a distinct species and none of the published specific epithets seems ap-

plicable to a blunt-leaved entity, elevation of var. *microphylla* to species rank is unavoidable.

Klainedoxa microphylla (Pellegrin) A. Gentry, comb. et stat. nov., *K. gabonensis* var. *microphylla* Pellegrin, Bull. Soc. Bot. France 71: 54. 1924. TYPE: Gabon. Maboumi *LeTestu 1823* (P, not seen).

This is apparently the same taxon as the "imperfectly known" *Klainedoxa* species from Ghana mentioned in the "Flora of West Tropical Africa." It is possible that the earlier name *K. sphaerocarpa* Tieghem (1905: 303) applies to this taxon. However, that species was based entirely on fallen fruits, described as spherical and 3–4 cm in diameter. Since the fruits that constitute the type of *K. sphaerocarpa* are apparently no longer extant (Letouzey, pers. comm.), and since aberrant or immature fruits of either *K. trillesii* or *K. gabonensis* could also fit the inadequate description, it seems preferable to raise the well-known and well-typified var. *microphylla* to specific rank rather than resurrect the undocumented epithet *sphaerocarpa*.

The three species of *Klainedoxa* at Makokou (and in the world) may be separated by the following key. Note that the leaf dimensions refer only to mature leaves. The juvenile leaves of *K. microphylla* and *K. trillesii* are unknown. However, since juvenile leaves of *K. gabonensis* are often much larger than mature leaves, it is likely that the same will prove true for the other two species. If so, their juvenile leaf dimensions may overlap with those of *K. gabonensis*.

KEY TO SPECIES

1. Leaves obtuse at apex, elliptic to obovate; fruits globose, 3.5–4.5 cm in diameter, glaucous gray-green *K. microphylla*
- 1'. Leaves acute at apex, ovate to ovate-lanceolate; fruits depressed-globose, distinctly broader than long, 5-angled, not glaucous.
 2. Mature leaves mostly less than 9 cm long (a few rarely to 11 cm long) and 5(–6) cm wide; fruits less than 3 cm long and 4 cm wide, turning yellow at maturity *K. trillesii*
 - 2'. Leaves mostly more than 9 cm long and (4–)5 cm wide; fruits 4–4.5 cm long and 5–7 cm wide, green at maturity *K. gabonensis*

Since no attempt has been made to study all extant material of *Klainedoxa*, it may seem pre-

mature to apply the Makokou results to the entire genus throughout its geographic range. However, all available evidence suggests that there is no breakdown of the key differentiating characters elsewhere in Africa, despite the notorious intra-specific variability of *K. gabonensis*. Moreover, the three Makokou taxa clearly "pass the test of sympatry," mandating taxonomic recognition at the species level even were the species limits obscured elsewhere. By definition subspecies are allopatrically distributed variants. Recognition of the three Makokou taxa at varietal level would imply differences in only a few genes, clearly incompatible with the whole suite of consistent differentiating characters in both fruit and leaves reported here.

LITERATURE CITED

- AUBRÉVILLE, A. 1962. Irvingiaceae. In *Flore du Gabon* 3: 12–32.
- ENGLER, A. 1907. Simarubaceae africanae II. Bot. Jahrb. Syst. 39: 575.
- . 1911. Simarubaceae africanae III. Bot. Jahrb. Syst. 46: 285.
- FLORENCE, J. & A. HLADIK. 1980. Catalogue des phanérogames et des ptéridophytes du nord-est du Gabon (Sixième liste). *Adansonia*, Sér. 2, 20: 235–253.
- GILBERT, G. 1958. Irvingiaceae. In *Flore du Congo Belge et du Ruanda-Urundi* 7: 109–118.
- HALLÉ, N. 1964. Liste de phanérogames et de ptéridophytes des environs de Makokou, Kemboma et Bélinga. *Biol. Gabon*. 1: 41–46.
- . 1965. Seconde liste de phanérogames et ptéridophytes du N.-E. Gabon (Makokou, Bélinga, et Mékambo). *Biol. Gabon*. 2: 337–344.
- & A. LE THOMAS. 1967. Troisième liste de phanérogames du N.-E. Gabon (Makokou, Bélinga, et Mékambo). *Biol. Gabon*. 3: 113–120.
- & ———. 1970. Quatrième liste de phanérogames et ptéridophytes du N.-E. du Gabon (Bassin du L'Ivindo). *Biol. Gabon*. 6: 131–138.
- HLADIK, A. & N. HALLÉ. 1973. Catalogue des phanérogames du nord-est du Gabon (Cinquième liste). *Adansonia*, Sér. 2, 13: 527–544.
- HUTCHINSON, J. & J. M. DALZIEL. 1958. *Flora of West Tropical Africa*. 2nd edition. 1(2): 692–694.
- LETOUZEY, R. 1975. Premières observations concernant au Cameroun la forêt sur cordons littoraux sablonneux. *Adansonia*, Sér. 2, 14: 529–542.
- PELLEGRIN, F. 1924. Remarques critiques sur les espèces du genre *Klainedoxa* Pierre. Bull. Soc. Bot. France 71: 51–56.
- TIEGHEM, P. VAN. 1905. Sur les Irvingiacées. *Ann. Sci. Nat. Bot.*, Ser. 9, 1: 245–320.

NOTE ADDED IN PROOF: After reading this manuscript, John Hart and Terese Hart inform me that they independently recognized the same three sympatric species of *Klainedoxa* while studying ungulate dispersal in the Ituri Forest of Zaire.